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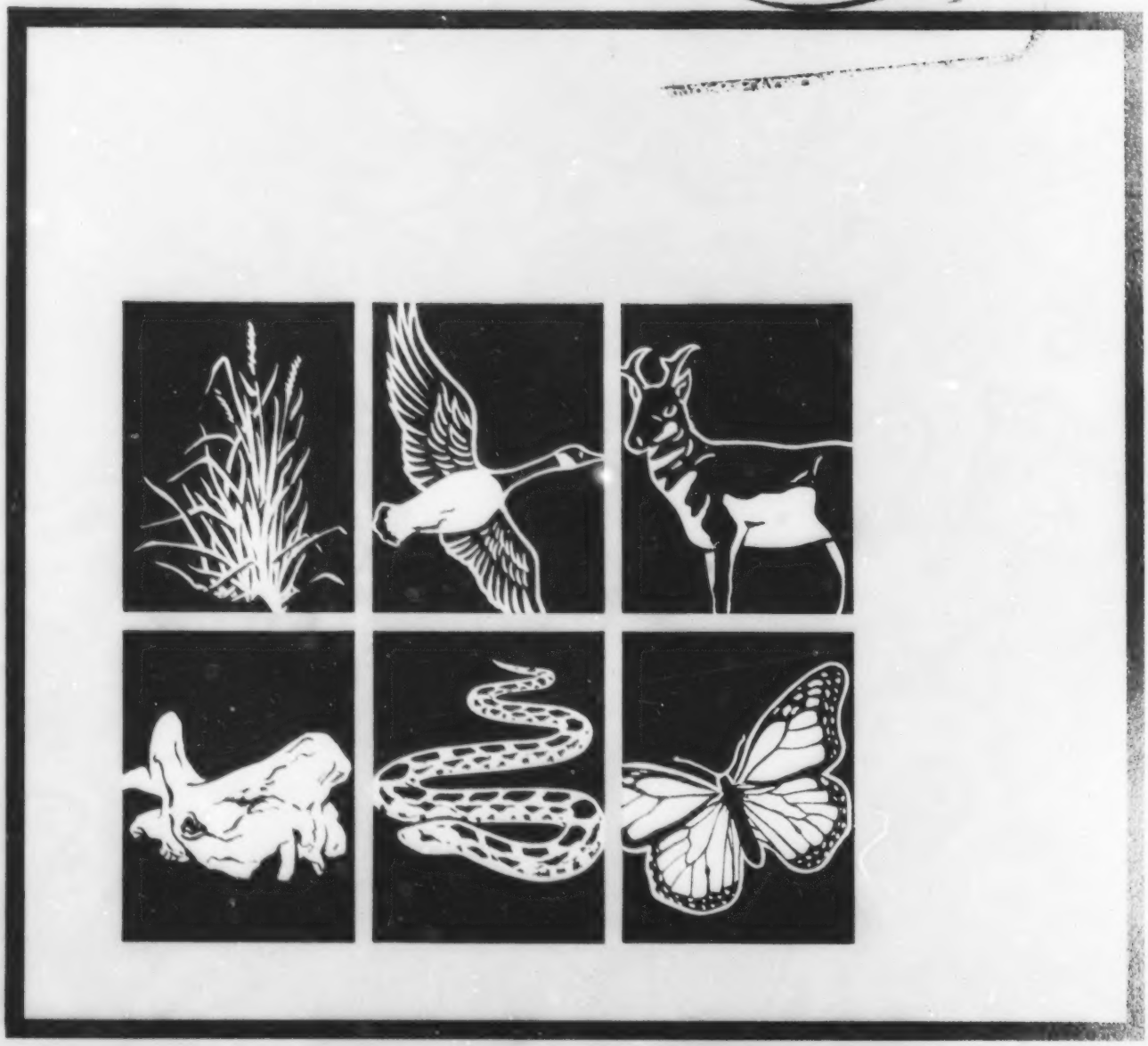
Leptomerycid Artiodactyla of the Calf Creek Local Fauna
(Cypress Hills Formation, Oligocene, Chadronian)
Saskatchewan



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Natural History Contributions No. 3

Leptomerycid Artiodactyla of the Calf Creek Local Fauna (Cypress Hills Formation, Oligocene, Chadronian) Saskatchewan

by John E. Storer

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Leptomerycid Artiodactyla of the Calf Creek Local Fauna (Cypress Hills Formation, Oligocene, Chadronian) Saskatchewan

John E. Storer

Three artiodactyl taxa that occur in the Calf Creek Local Fauna, *Hendryomeryx esulcatus* (Cope), *Leptomeryx speciosus* Lambe, and *Leptomeryx mammifer* Cope, are valid species properly assigned to the family Leptomerycidae. Size, height of crown, and details of crown construction separate the taxa from each other and from other named leptomerycid species. *Leptomeryx speciosus* and *Leptomeryx mammifer* are also recognized from Pipestone Springs, Montana and Flagstaff Rim, Wyoming.
(Artiodactyla: Leptomerycidae: Oligocene: Saskatchewan)

INTRODUCTION

Teeth of leptomerycid artiodactyls are the most common mammalian fossils in the Cypress Hills Oligocene, but relatively little has been written about them.

Lack of clarification of the Cypress Hills taxa has posed a serious problem for paleomammalogists. The three senior names for Chadronian leptomerycid species are based on scanty (in fact barely determinate) Cypress Hills material, and it has been impossible to identify or describe Chadronian specimens satisfactorily without much more knowledge of the Cypress Hills taxa than has been available.

The three taxa discussed here are, in order of increasing size, *Hendryomeryx esulcatus* (Cope) 1889; *Leptomeryx speciosus* Lambe 1908; and *Leptomeryx mammifer* Cope 1885.

Another species whose reference to the Leptomerycidae has been challenged by many authors is *Leptomeryx semicinctus* Cope 1889. This taxon is actually a protoceratid, and additional material will be described in another paper.

METHODS AND MATERIALS

I have characterized the Cypress Hills Oligocene leptomerycid taxa using Saskatchewan Museum of Natural History (SMNH) specimens from the Calf Creek Local Fauna. Background data on SMNH fossils considered here (prefix P) were given in an earlier paper (Storer 1978)

Holotypes of all three taxa discussed are deposited in the Vertebrate Paleontology collections, National Museum of Natural Sciences, National Museums of Canada (NMC).

Illustrations were made by Mr. James S. McLean, Moose Jaw. Relative sizes of specimens are indicated by 1 mm scale bars.

All dental measurements are maxima for the crown, were made with hand-held dial calipers (Fowler type 6921), and are given to the nearest 0.1 mm.

Measurements of crown height were taken on unworn or nearly unworn permanent teeth. The crown height measurement represents the distance from the base of the enamel to the tip of the paracone in upper cheek teeth, the protoconid in lower premolars, and the metaconid in lower molars.

For measurements in paragraph form, the object measured is given first, then the measurement (AP, anteroposterior diameter; BL, buccolingual diameter;

HC, height of crown), with number of specimens in parentheses, and mean, observed range (OR), and coefficient of variation (CV).

SYSTEMATIC DESCRIPTION

Family Leptomerycidae

Genus *Hendryomeryx* Black 1978

Hendryomeryx esulcatus (Cope) 1889, new combination

Leptomeryx esulcatus Cope 1889, p. 154

Holotype: $RM^?$, NMC 6277.

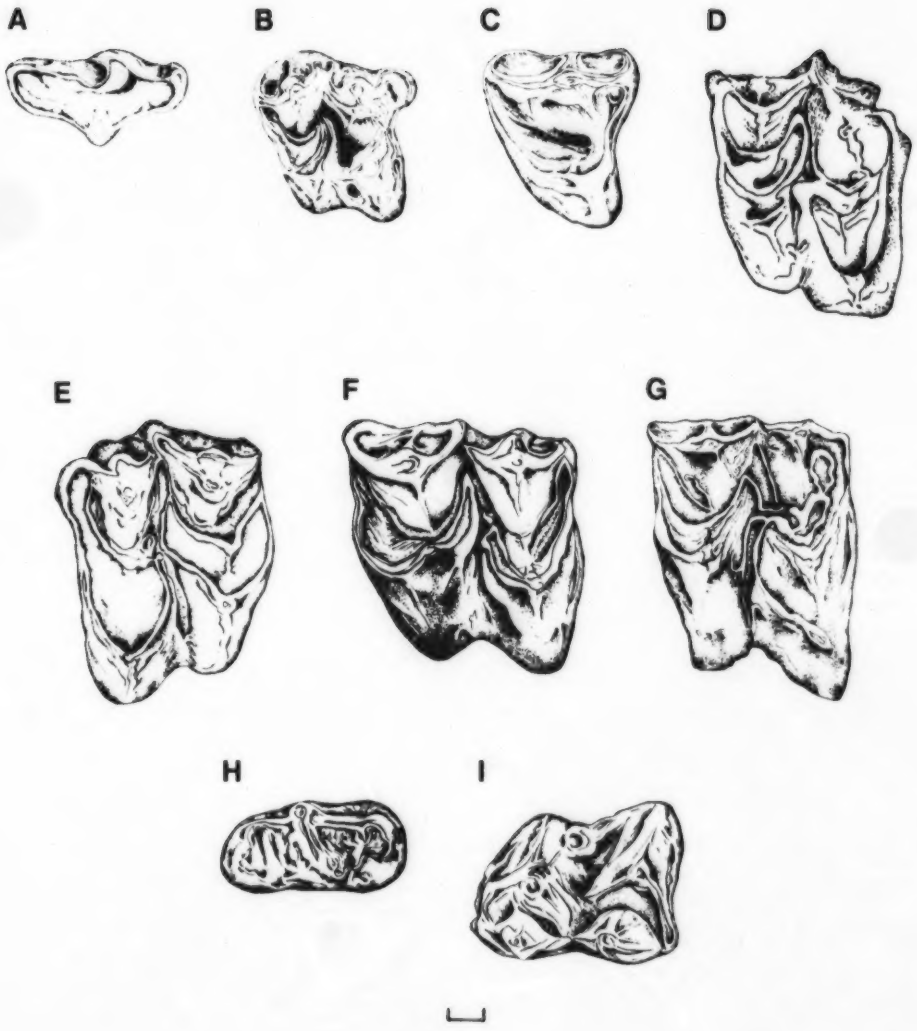
Referred specimens: LP^2, P661.681; RP^2, P661.683-684; LdP^3, P661.685; LP^3, P661.686-687, P1585.1207; RdP^4, P661.688; LP^4, P661.690; RP^4, P661.689; $LM^?$, P661.691-697, P1585.1208-1209; $RM^?$, P661.698-702, P661.907, P661.927, P661.931, P1585.1210-1213; LP_2, P661.703; RP_4, P661.704-705; LM_1 or M_2, P661.707-715, P1585.1215-1218; RM_1 or M_2, P661.716-722, P1585.1219-1225; L. mandibular fragment with LM_1, P661.706; R. mandibular fragment with RM_1, P1585.1214.

Emended diagnosis: Size of *Hendryomeryx wilsoni;* teeth higher crowned than in that species; three-rooted P^2 with large but low lingual cusp; P^3 lingual cusp connected basally to paracone; M_{1-2} buccal column usually double.

Description: Permanent cheek teeth are low-crowned and shallow-patterned, and on the average are smaller than corresponding teeth of *Leptomeryx speciosus*.

P^2 (Fig. 1A) is three-rooted. The parastyle is strong, and there is a slight indication of a metacone, nearly submerged in the crest that runs posterad from the paracone. A prominent bulge in the middle of the

Fig. 1 *Hendryomeryx esulcatus*. Buccal to top of page, anterior to left in E,H,I, to right in A-D, F,G. Scale 1 mm.
A, RP^2, P661.683; B, RdP^4, P661.688; C, RP^4, P661.689; D, $RM^?$, NMC 6277 (holotype); E,$LM^?$, P661.697; F, $RM^?$, P661.907; G, $RM^?$, P1585.1210; H, RP_4, P661.704; I, RM_1, P1585.1214.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lingual face represents the lingual cusp, which is very weak and low. The lingual cingulum is complete, and is strong posterior to the lingual cusp, but is very weak anterior to the lingual cusp.

The only preserved dP^3 is worn, and is missing its anterior end. It does not differ substantially in visible features from dP^3 of *Leptomeryx speciosus*.

None of the P^3 specimens is well preserved. The lingual cusp is large and strong, connected basally to the paracone. Paracone and parastyle are close together, and the lingual cingulum is strong and continuous.

dP^4 (Fig. 1B) is molariform, and shows even shorter crown height and shallower pattern than in *L. speciosus*. All buccal styles are stronger than in the permanent upper molars, and the column in the lingual valley is weak. There is a small cuspule at the posterolingual edge of the paracone, as in M^{1-3}.

In P^4 (Fig. 1C), the paracone is high and sharp, the parastyle is low but distinct, and no metacone occurs. There are very weak traces of anterior and posterior cingula at the base of the lingual cusp.

Permanent upper molars (Fig. 1D-G) show a cuspule at the posterolingual edge of the paracone, joining in late wear (Fig. 1G) with the anterior metaconule arm. Parastyle and mesostyle are prominent, the metastyle is small. The rib on the buccal face of the metacone is less well defined than the external paracone rib, and on most specimens is poorly demarcated. The column in the lingual valley is small and low.

Only a fragment of P_2 is preserved. A single talonid ridge connects with the lingual portion of the

protoconid, and runs to the posterobuccal corner of the crown.

In P_4 (Fig. 1H) the metaconid is only slightly smaller and lower than the protoconid. The paraconid is sharply inflected, and the talonid is complex and closed posteriorly.

First and second lower molars (Fig. 1I) show no lingual stylids. Anterior and posterior cingula are small. A low buccal column, usually double, blocks the buccal valley. The anterior crest of the hypoconid is straight, and drops sharply to meet the posterior protoconid crest about mid-height.

Discussion: Re-examination of Cope's holotype (Fig. 1D) shows that this species is definitely referable to *Hendryomeryx* Black (1978). NMC 6277, a right permanent upper molar, is lower crowned than in species of *Leptomeryx*, has a short postprotocrista directed posterad, and shows the characteristic cuspule posterolingual to the paracone. Cope's diagnostic characteristic, "the absence of sulci which define an external rib" on buccal cusps (1891, p. 22), can no longer be observed on the holotype, but is also typical of *Hendryomeryx* rather than *Leptomeryx*.

Permanent cheek teeth are only slightly lower crowned, proportionally, than corresponding teeth of *Leptomeryx speciousus* from the Calf Creek Local Fauna. Molars are, however, much shallower-patterned than in *Leptomeryx*, with the bottoms of the fossettes and fossettids easily visible: in *Leptomeryx*, valley walls are much steeper, and valley bottoms are not easily visible except in very worn specimens. The comparison in pattern depth between *Hendryomeryx* and

Leptomeryx is much like that used to separate *Pseudocylindrodon* and *Cylindrodon* (Burke 1935).

Another feature of lower molars that I have used to identify *Hendryomeryx* teeth in the Calf Creek sample is the low hypoconid-protoconid connection. In little-worn *Hendryomeryx* lower molars from Calf Creek, it is possible to sight along a line from the tip of the buccal column to the ridge that connects the metaconid and entoconid. The anterior hypoconid arm dips so sharply that it does not block that line of sight: in *Leptomeryx speciosus* the anterior hypoconid arm is much higher, and always blocks such a line of sight.

Hendryomeryx esulcatus overlaps in size with *Leptomeryx speciosus*, though means of its linear dimensions are smaller. The two species are separated on details of occlusal pattern described above. The holotype upper molar of *H. esulcatus*, NMC 6277 (AP, 6.0; BL, 6.6) is near the lower end of the size range for the Calf Creek sample, and is smaller than any upper molar referred to *L. speciosus*.

Hendryomeryx esulcatus is the senior specific name for the genus. *H. wilsoni* Black 1978 and *H. defordi* (Wilson) 1974 occur in earlier faunas, and apparently the three species are all valid, differing from each other in subtle ways. The relationships of these taxa, and of other, undescribed samples that presumably exist in Chadronian collections, will be difficult to analyze.

Matthew's provisional use of the name *Leptomeryx esulcatus* for the smaller of the two *Leptomeryx* species from Pipestone Springs, Montana (1903, p.222-223) was

not justified in terms of what we now know about the taxon. I have seen no Pipestone specimen that shows the small size, low crown, or shallow occlusal pattern of *H. esulcatus*. As noted elsewhere in this paper, the smaller Pipestone Springs species is *Leptomeryx speciosus*.

Scaled P^2-M^3 and P_2-M_3 lengths for *H. esulcatus* are: P^2-M^3, approximately 29 to 40 mm; P_2-M_3, approximately 32.5 to 41.5 mm. These extrapolations were made by comparison with *Leptomeryx* tooth rows lent for study by Dr. R. J. Emry, Smithsonian Institution, and are intended only as general estimates of size.

Measurements: P^2, AP(1), 5.2; BL(3), mean 2.7, OR 2.4-3.0; HC(1), 2.7. dP^3, BL(1), 2.5. P^3, AP(1), 5.6; BL(3), mean 3.7, OR 3.4-3.9. dP^4, AP(1), 4.7; BL(1), 4.4. P^4, AP(2), mean 4.4, OR 4.2-4.5; BL(1), 5.0; HC(1), 3.6. $M^?$, AP(21), mean 6.4, OR 5.5-7.4, CV 7.8; BL(17), mean 7.9, OR 6.5-9.5, CV 10.1; HC(4), mean 3.8, OR 3.5-4.2. P_2, BL(1), 1.1. P_4, AP(1), 5.3; BL(2), mean 2.4, OR 2.2-2.5: HC(2), mean 3.4, OR 3.3-3.5. M_1, AP(2), mean 6.4, OR 6.0-6.8; BL(2), mean 4.4, OR 4.1-4.6; HC(2), mean 3.9, OR 3.6-4.1. M_1 or M_2, AP (26), mean 6.5, OR 5.6-7.8, CV 9.2; BL(27), mean 4.5, OR 3.8-5.4, CV 8.9; HC(12), mean 4.3, OR 3.9-4.7, CV 4.7.

Genus *Leptomeryx* Leidy 1853
Leptomeryx speciosus Lambe 1908
Holotype: $RM^?$, NMC 6311

Referred specimens: LdP^2, P661.732-744, P661.761, P1585.1231; RdP^2, P661.745-757, P1585.1232; LP^2, P661.758-760, P661.762-782, P661.838, P1585.1233-1236, P1585.1245, P1585.1251; RP^2, P661.783-798, P1585.1237-

1244; LdP^3, P661.799-808, P1585.1246; RdP^3, P661.809-813, P661.815-816, P1585.1247-1248; LP^3, P661.814, P661.817-837, P661.839, P1585.1249-1250, P1585.1252-1257; RP^3, P661.840-858, P1585.1256, P1585.1259-1261; LdP^4, P661.859-884, P1585.1263-1269; RdP^4, P661.885-888, P661.890-906, P661.908-915, P661.917-926, P661.928-930, P661.932, P1585.1271-1272; LP^4, P661.933-950, P1585.1273-1279; RP^4, P661.951-975, P1585.1280-1283; $LM^?$, P661.976-1041, P1585.1262, P1585.1285-1323; $RM^?$, P661.916, P661.1042-1107, P1585.1324-1353; L. maxillary fragment with LP^4-LM^1, P661.1108; LdP_2, P661.1109-1112, P1585.1354; RdP_2, P661.1113-1119, P1585.1355-1357; LP_2, P661.1120-1137, P1585.1358-1359; RP_2, P661.1138-1158, P1585.1360-1361; LdP_3, P661.1159-1176; RdP_3, P661.1177-1188; LP_3, 1189-1208, P1585.1362-1366; RP_3, P661.1209-1238, P1585.1367-1376; LdP_4, P661.1239-1257, P1585.1377; RdP_4,P661.1258-1273, P1585.1378; LP_4, P661.1274-1303, P661.1306, P1585.1379-1390; RP_4, P661.1304-1305, P661.1307-1332, P1585.1391-1397; LM_1 or M_2, P661.1333-1392, P1585.1398-1422; RM_1 or M_2, P661.1393-1441, P1585.1423-1459; LM_3, P661.1442-1461, P1585.1460-1471; RM_3, P661.1462-1474, P1585.1472-1477; R. mandibular fragment with RP_{2-3}, P661.1475; L. mandibular fragment with LP_{3-4}, P661.1476; L. mandibular fragment with LP_4-LM_1, P661.1477; R. mandibular fragment with RP_4-RM_1, P661.1478; L. mandibular fragment with LP_4-LM_2, P661.1479; L. mandibular fragment with LP_4-LM_3, P1585.1479; R. mandibular fragment with RP_4-RM_3, P661.1487; L. mandibular fragment with LM_1, P661.1480-1481; R. mandibular fragment with RM_1, P1585.1478; L. mandibular fragment with LM_{1-2}, P1585.1480; R. mandibular fragment with RM_{1-2}, P661.1482-1483; R. mandibular

fragment with RM_{1-3}, P661.1484-1485; R. mandibular fragment with RM_{2-3}, P661.1486.

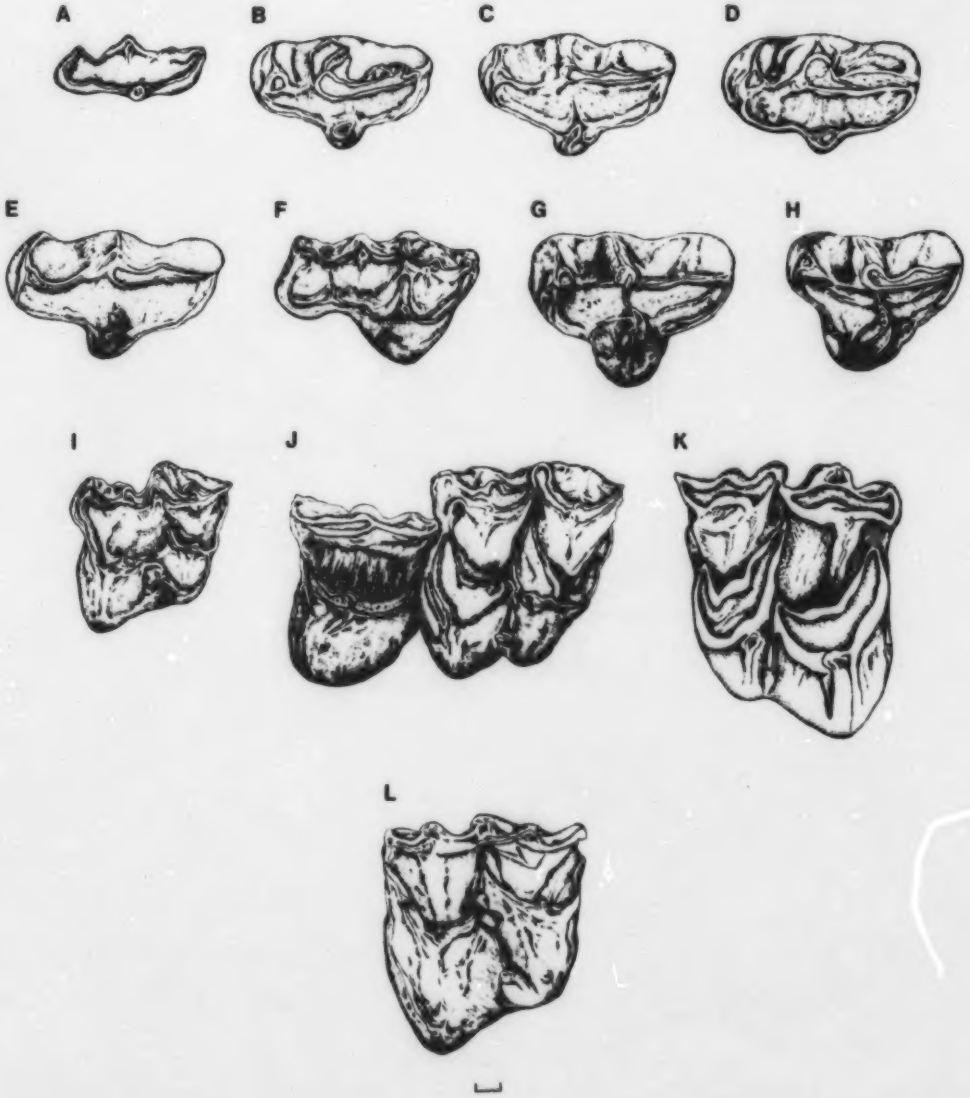
Emended diagnosis: Permanent cheek teeth brachydont, but not as low crowned or shallow patterned as in *Hendryomeryx*; P^2 three-rooted, with prominent lingual cusp; upper molars with buccal styles not as strong as in *L. mammifer*; principal talonid elements of P_{2-3} connect to lingual portion of protoconid; P_2 with large, conical paraconid; P_3 forms closed basin posterior to protoconid in many specimens; P_4 hypoconid usually with strong buccal projection forming strong "heel."

Description: dP^2 (Fig. 2A) is long, narrow, and two-rooted. The paracone is high and sharp, set just anterior to the middle of the buccal wall, and the parastyle is prominent. An indistinct metacone is nearly submerged in the crest that extends posterad from the paracone. The lingual cingulum is strong and complete.

About half the specimens at hand (15 of 29) show a central bulge in the lingual crown face and a thickening of the lingual cingulum, or show a distinct lingual cusp. The rest have a continuous lingual cingulum with no lingual cusp.

P^2 (Fig. 2B-E) is three-rooted and is narrow, though proportionally wider than dP^2 because of the prominent lingual cusp, which is strongly, faintly, or not connected to the protocone base. The paracone is high and sharp, the parastyle prominent and bulbous, and the metacone small. A strong lingual cingulum is usually complete, but in a few specimens shows a gap immediately posterior to the lingual cusp. The shape

Fig. 2. *Leptomeryx speciosus*. Upper cheek teeth. Buccal to top of page, anterior to left in A-J, L, to right in K. Scale 1 mm. A, LdP^2, P661.735; B, LP^2, P661.758; C, LP^2, P661.759; D, LP^2, P661.760; E, LP^2, P661.762; F, LdP^3, P661.801; G, LP^3, P661.818; H, LP^3, P1585.1249; I, LdP^4, P1585.1266; J, LP^4-M^1, P661.1108; K, $RM^?$, NMC 6311 (holotype); L, $LM^?$, P1585.1323.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of this tooth and the sharpness of the lingual indentations vary somewhat, although lingual indentations are generally sharp. Accessory cuspules appear in a few specimens, in the buccal valleys and along the lingual cingulum. Accessory ridges may occur on the buccal faces of the paracone and parastyle.

In the three-rooted dP^3 (Fig. 2F) the sharp metacone is the highest cusp, and the meso-and metastyles are prominent. The second-highest cusp is the paracone, which is anteroposteriorly elongate. A triangular parastyle is nearly as high as the metacone and paracone. The metaconule is also triangular, and is strongly connected to the anterolingual face of the metacone, the metastyle, and the anterior cingulum. If a protocone (or lingual cusp) is present, it may be represented by either of two small cusps along the complete, strong lingual cingulum. Accessory cuspules are common along the crown border. The posterior cingulum is short and indistinct. Many variations in shape of dP^3 exist in this sample, dependent mainly on the size and shape of the metaconule.

P^3 (Fig.2G-H) basically resembles P^2, but the lingual cusp is much larger and the crown is relatively much broader. A large accessory cuspule commonly occurs posterior to the lingual cusp, at its connection with the lingual cingulum, and occasionally an accessory cuspule occurs anterior to the lingual cusp.

In dP^4 (Fig. 2I) the paracone and metacone are of approximately the same shape and height, and the buccal styles are large and prominent. The metaconule is strongly connected to both the metastyle and the anterolingual corner of the metacone. A strong proto-

cone is strongly connected to the parastyle and metaconule. A low, transversely elongate column blocks the lingual valley anterolingual to the metaconule. The anterior cingulum is long and slender, the posterior cingulum indistinct. A few specimens show the small accessory cuspule at the posterolingual base of the paracone that has been described in *Hendryomeryx*.

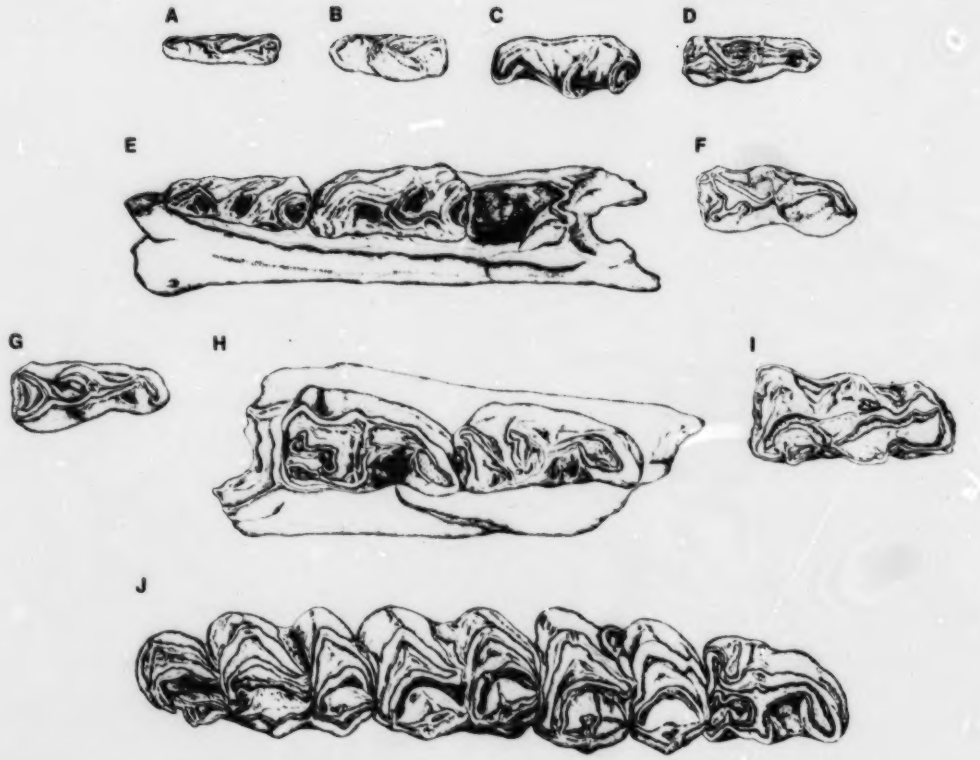
In P^4 (Fig. 2J) the paracone is high, the parastyle low but clearly separate from the paracone, and the metacone small to prominent. Small anterior and posterior cingula occupy the base of the lingual cusp.

Upper molars (Fig. 2J-L) are of moderate crown height, have strong buccal styles, and show well-defined ridges on the buccal sides of the paracone and metacone. An anterior cingulum is short but well defined, and a short column at the anterolingual corner of the metaconule blocks the lingual valley. The posterior arm of the protocone is inflected buccally. Enamel rugosity and accessory ridges into fossettes vary.

Some upper molars (Fig.2L) show a straightened ectoloph, a low mesostyle, or a continuous cingulum around the lingual face of the protocone. A few of these may be misidentified teeth of small protoceratids, especially if the postprotocrista is relatively long. Similar variants do occur in other leptomerycid samples, however, and identification is certain only when the premolars are preserved with the molars, a luxury that students of Cypress Hills vertebrates seldom enjoy.

dP_2 (Fig. 3A-B) is smaller and proportionally narrower than P_2. The principal talonid ridge arises from the middle or the lingual edge of the protoconid,

Fig. 3. *Leptomeryx speciosus*. Lower cheek teeth. Buccal to top of page, anterior to left in A-C, E, to right in D, F-J. Scale 1 mm. A, RdP_2, P661.1113; B, RdP_2, P661.1114; C, RP_2, P1585.1360; D, LdP_3, P661.1160; E, RP_{2-3}, P661.1475; F, LP_3, P661.1189; G, LP_3, P661.1192; H, LP_{3-4}, P661.1476; I, LdP_4, P661.1256; J, LP_4, M_{1-3}, P1585.1479.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and curves to near the posterobuccal corner of the crown. A shorter, secondary talonid ridge arises near the posterior end of the principal talonid ridge, and is directed posterolinguad. The paraconid is strong and bulbous.

In P_2 (Fig. 3C,E) the protoconid is the highest cusp. A ridge extends anterobuccad to the large, conical paraconid. A buccal ridge from the protoconid dips ventrad and runs posterobuccad, then straight ventrad to the base of the crown. The principal talonid ridge arises near the lingual edge of the protoconid, often with a short ridge lingual to it, and curves to near the posterobuccal corner of the crown. A short secondary talonid ridge arises near the posterior end of the principal talonid ridge, and is directed posterolinguad. A low cingulum connects the talonid ridges at the posterior crown border in most specimens, forming a shallow, closed basin.

dP_3 (Fig. 3D) is much like dP_2. The secondary talonid ridge reaches the posterolingual corner of the crown, and in many specimens a prominent cuspule lies between the posterior ends of the talonid ridges. In most specimens the buccal ridge from the protoconid curves toward the junction of the talonid ridges, forming a closed basin just posterior to the protoconid.

P_3 (Fig. 3E-H) resembles P_2, but is comparatively broader, especially at the posterior end. There is a prominent buccal cingulum at the anterobuccal edge of the paraconid. The buccal ridge from the protoconid is higher above the crown base than in P_2, and often curves linguad to form a closed basin immediately posterior to the protoconid. As in P_2, there are often

additional accessory ridges from the protoconid.

dP_4 (Fig. 3I) is an elongate, three-rooted tooth that tapers gradually from posterior to anterior. No lingual stylids are evident. A posterior cingulum is prominent, and is often made up of a series of cuspules, but the anterior cingulum is short and weak. The anterior arm of the hypoconid is connected to a spur from the protoconid. The protoconid-metaconid connection is strong. Prominent buccal cuspules occur between the protoconid and hypoconid, and between the anteroconid and protoconid. The lingual portion of the anteroconid is larger than the buccal portion.

P_4 (Fig. 3H,J) is a broad, robust tooth. A prominent buccal cingulum occupies the anterobuccal edge of the paraconid. The metaconid is nearly as large as the protoconid, and is set nearly directly lingual to it. A strong ridge connects the protoconid and hypoconid, and the metaconid-entoconid connection is not quite as strong. The hypoconid has a strong buccal projection, set off from the protoconid by a sharp valley, that forms a strong "heel" in worn teeth. A spur from the hypoconid connects mid-height with the entoconid, closing the talonid basin posteriorly in medium and advanced wear stages. An accessory ridge from the anterior end of the hypoconid is directed toward the entoconid.

In lower molars (Fig. 3J), protoconid-metaconid connections are strong, and lingual stylids are not apparent. The anterior arm of the hypoconid connects high to the posterior arm of the protoconid. Posterior cingula are weak, anterior cingula are short. The protoconid-hypoconid valley is blocked by a column that

is usually smaller in M_2 than in M_1, and smaller in M_3 than in M_2.

The posterior lophid of M_3 is composed of a strong buccal cusp, connected strongly anteriorly to the posterior arm of the hypoconid, and a weaker but prominent lingual cusp, connected strongly to the entoconid. The posterior arm of the hypoconid points toward the anterior end of the posterolingual cusp, and is sometimes connected to a spur from the entoconid. There is no basal column between the hypoconid and the posterior lophid.

Discussion: *Leptomeryx speciosus* is by far the most common fossil mammal in the Cypress Hills Chadronian deposits. Nearly all specimens assigned to the species are isolated teeth, and associated specimens are very rare in this formation.

The holotype upper molar of *Leptomeryx speciosus*, NMC 6311 (AP,7,8; BL,10.2) is near the mean size for the Calf Creek sample. Measurements of the holotypes of *Hendryomeryx esulcatus* and *Leptomeryx mammifer* fall well outside the ranges for *L. speciosus*.

Matthew (1903, p. 223) was the first to point out a major dissimilarity between Chadronian *Leptomeryx* species and the Orellan *Leptomeryx evansi:* "In the third lower premolar the protoconid has two posterior ridges, of which the internal one connects with the heel, and the external one does not; while in *L. evansi* and other species from the Oreodon and Leptauchenia Beds, the external ridge connects with the heel, and the internal one does not." *L. speciosus* from the Calf Creek Local Fauna is of the Chadronian type, although the common variant in P_3 and its deciduous precursor, in which a closed basin is formed posterior to the

protocone, may represent an intermediate in evolutionary grade, for this feature, between the Chadronian forms and *L. evansi*.

The material at hand also differs from *L. evansi* in that P^2 is always three-rooted: Scott (1940, p.538) described the tooth as two-rooted in *L. evansi*. It would also appear from Clark and Guensberg's measurements of metaconid height in M_{1-3} (1970) that *L. evansi* is lower crowned than *L. speciosus*. *L. evansi* has not been thoroughly studied since Scott's work, and it is likely that further comparison would reveal other differences in detail.

Of the described Chadronian leptomerycids, *Hendryomeryx esulcatus*, discussed earlier in this publication, is generally smaller and lower crowned, and much shallower patterned than *L. speciosus*, and differs in other details as discussed.

Leptomeryx mammifer, discussed later, is larger and higher crowned than *L. speciosus*, and shows stronger buccal styles in upper molars. Buccal columns in lower molars of *L. mammifer* are weak or absent.

Leptomeryx yoderi Schlaikjer (1935) is difficult to distinguish from *L. speciosus*, and confusion between the taxa will inevitably arise unless the key distinguishing features are preserved. Teeth of the two species are of nearly the same mean size and crown height. *L. yoderi* shows a tiny, low paraconid in P_2, as compared with the large, conical paraconid in *L. speciosus*. In *L. yoderi* the "heel" of the P_4 hypoconid is not as prominent or as sharply set off from the protoconid as in *L. speciosus*, although this feature is variable in *L. speciosus*. I have not seen the variant

of P_3 showing a closed basin behind the protoconid in the limited sample of *L. yoderi* I have examined.

I hope that detailed study of *Leptomeryx yoderi* will reveal additional diagnostic differences from *L. speciosus*. At present it appears that the species are separate, but distinguishable only with difficulty.

Leptomeryx antecedens Cook (1934) is not well known, and I have not examined the holotype. The taxon as described by Cook has a small, anteroposteriorly compressed posterior lophid on M_3, unlike all other known leptomerycids including *L. speciosus*. *L. antecedens* is much smaller than *L. speciosus*, and the holotype is approximately the size of a small *Hendryomeryx esulcatus*: Cook thought that it was also brachydont.

Lambe (1908, p.31), in his original description of *Leptomeryx speciosus*, suggested that this species might be the correct reference for specimens from Pipestone Springs, Montana that Matthew (1903, p.222-223) had referred provisionally to *Leptomeryx esulcatus*. His suggestion has never been implemented formally, probably because so little was known about the Cypress Hills taxa.

Russell's description and illustration of *L. speciosus* P_2 to M_1 (1934, p.64; fig. 7) greatly clarified resemblances to the smaller Pipestone Springs leptomerycid. Now with more Cypress Hills material available than before, my comparisons with Pipestone specimens are yet more conclusive.

The smaller Pipestone leptomerycid is clearly not referable to *Hendryomeryx esulcatus*, for reasons specified earlier. The Pipestone sample does agree

with Cypress Hills *Leptomeryx speciosus* in size, height of crown, depth of pattern, and other diagnostic features, and should certainly be referred to that species.

Likewise, Emry's "Species E" (1973, p.34) from Flagstaff Rim, Wyoming, is probably *L. speciosus*, because he stated that it compared closely with the smaller form from Pipestone Springs.

Scaled tooth-row lengths for Calf Creek *L. speciosus* (see note under *H. esulcatus*) are: P^2-M^3, approximately 34 to 47 mm; P_2-M_3, approximately 38 to 52.5 mm. Measurements: dP^2, AP(23), mean 5.9, OR 5.2-6.5, CV 6.8; BL(29), mean 2.3, OR 1.8-2.9, CV 8.7. P^2, AP(45), mean 7.2, OR 6.3-8.0, CV 6.9; BL(49), mean 4.2, OR 3.2-5.1, CV 9.5; HC(18), mean 3.6 , OR 3.1-4.0, CV 8.3. dP^3, AP(17), mean 7.0, OR 6.2-7.6, CV 4.3; BL(19), mean 4.4, OR 3.6-5.0, CV 9.1. P^3, AP(49), mean 7.4, OR 6.2-8.0, CV 5.4; BL(44), mean 5.5, OR 4.6-6.4, CV 7.3; HC(11), mean 4.4, OR 4.1-5.4, CV 9.1. dP^4, AP(76), mean 6.2, OR 5.2-6.8, CV 4.8; BL(61), mean 6.7, OR 5.2-7.9, CV 7.5. P^4, AP(55), mean 5.3, OR 4.7-6.4, CV 5.7; BL(48), mean 6.8, OR 5.8-7.5, CV 7.4; HC(17), mean 4.8; OR 3.9-5.5, CV 10.4. M^1, AP(1), 7.8; BL(1), 8.2. M^2, AP(180), mean 7.8, OR 6.4-9.3, CV 6.4; BL(160), mean 9.7, OR 7.7-11.4, CV 8.2; HC(52), mean 5.3, OR 4.4-6.3, CV 9.4. dP_2, AP(13), mean 5.0, OR 4.4-5.4, CV 6.0; BL(13), mean 1.6, OR 1.2-1.9, CV 12.5. P_2, AP(34), mean 6.0, OR 5.4-6.6, CV 5.0; BL(43), mean 2.2, OR 1.7-2.5, CV 9.1; HC(19), mean 3.2, OR 2.6-3.5, CV 6.3. dP_3, AP(19), mean 6.0, OR 5.4-6.5, CV 5.0; BL(30), mean 2.1, OR 1.9-2.5, CV 4.8. P_3, AP(49), mean 6.7, OR 5.7-7.8, CV 6.0; BL(67), mean 2.8, OR 2.2-3.4, CV 10.7;

HC(25), mean 4.0, OR 3.1-4.7, CV 10.0. dP_4, AP(8), mean 8.3, OR 7.7-8.6, CV 3.6; BL(34), mean 3.9, OR 3.3-4.4, CV 7.7. P_4, AP(63), mean 7.0, OR 5.7-7.8, CV 7.1; BL(74), mean 3.7, OR 2.7-4.4, CV 8.1; HC(20), mean 4.9, OR 3.9-5.7, CV 10.2. M_1, AP(12), mean 7.9, OR 7.2-8.8, CV 5.1; BL(13), mean 5.4, OR 4.2-5.9, CV 9.3. M_2, AP(8), mean 8.5, OR 7.3-9.5, CV 7.1; BL(8), mean 5.8, OR 4.8-6.5, CV 8.6. M_1 or M_2, AP(161), mean 8.0, OR 6.5-9.2, CV 7.5; BL(167), mean 5.6, OR 4.5-7.4, CV 8.9; HC(51), mean 5.6, OR 4.4-6.4, CV 8.9. M_3, AP(37), mean 11.6, OR 10.4-12.5, CV 5.2; BL(54), mean 5.6, OR 4.6-6.5, CV 8.9; HC(16) mean 5.6, OR 4.7-6.4, CV 8.9.

Leptomeryx mammifer Cope 1885

Holotype: R. mandibular fragment with RM_{2-3}, NMC 6278.

Referred specimens: LdP^4, P1585.1284; RdP^4, P661.889, P1585.1270; $LM^?$, P661.723-725; $RM^?$, P661.726-731, P1585.1226-1228; LdP_4, P1585.1229; RM_3, P1585.1230.

Emended diagnosis: Buccal styles of upper molars very large and prominent; buccal columns of lower molars absent or very weak; teeth larger and higher crowned than in *Leptomeryx speciosus*.

Description: dP^4 resembles its counterpart in *Leptomeryx speciosus*, but is larger. Upper molars (Fig. 4A-B) show very strong buccal styles, especially the parastyle. Columns on the buccal faces of the para-and metacone are strong and very well defined. The anterior cingulum is strong and long. A strong lingual column, attached to the metaconule, blocks the

lingual valley, and a short cingulum at the base of the protocone attaches to it.

The available dP_4 is worn, and does not show all details. In observable features it closely resembles the corresponding tooth of *Leptomeryx speciosus*, but is much larger.

M_3 (Fig. 4C) shows no buccal column blocking the valley between the protoconid and hypoconid. The buccal cusp of the posterior lophid comes to a sharp point at the posterobuccal corner of the crown. Ridges on the lingual faces of the meta-and entoconids are well defined, especially near the tips of the cusps.

Discussion: Teeth of the holotype, NMC 6278 (M_2 AP, 10.2; BL, 6.5) are similar in size to the referred specimens, and M_2 shows greater anteroposterior diameter than any Calf Creek *L. speciosus*.

Although Cope's figured upper molar, NMC 6279 (1891, pl. 14, fig. 6), agrees in anteroposterior and buccolingual dimensions with *L. mammifer*, it is lower-crowned with bulbous cusps, and represents *Eotylopus*, an oromerycid. Cope's illustration, unfortunately, did not show occlusal detail adequately. Lambe (1908, p.31) formally designated the specimen as a paratype ("cotype"), which it cannot be.

Leptomeryx mammifer is very rare in the type area, and only 18 specimens were identified from the Calf Creek sample, compared with more than 1000 teeth of *L. speciosus*.

It is possible to get a little better idea of the nature of *L. mammifer* from this sample, though. The present specimens show large size, absence (or near

Fig. 4. *Leptomeryx mammifer*. Buccal to top of page, anterior to left in A,C,D, to right in B. Scale 1 mm. A, $LM^{?}$, P661.724; B, $RM^{?}$, P661.726; C, RM_3, P1585.1230; D, RM_2, broken M_1 and M_3, NMC 6278 (holotype).

A
B
C
D

absence) of buccal columns in lower molars, much higher crowns than in other Chadronian leptomerycids, and stronger buccal styles in upper molars. Molars of *L. mammifer* are also considerably higher crowned than molars of *L. speciosus*, and crown height is a characteristic that is diagnostic of this species.

As far as can be determined, the larger leptomerycid from Pipestone Springs, Montana, shows all these features, and Matthew's reference (1903) of Pipestone specimens to *Leptomeryx mammifer* was correct. Emry's "Species C" (1973, p.33), from Flagstaff Rim, Wyoming, is likewise referable to *L. mammifer*. It would be advantageous to extend the diagnosis based on referred material from Pipestone Springs and Flagstaff Rim, because of the rarity and incompleteness of specimens from the type area.

Approximate scaled tooth-row lengths for the holotype and for *L. mammifer* from Calf Creek (see note under *Hendryomeryx esulcatus*) are: P^2-M^3, approximately 56 to 57 mm; P_2-M_3, approximately 53 to 58 mm. Measurements: dP^4, AP(3), mean 7.6, OR 7.5-7.7; BL(2), mean 8.4, OR 8.3-8.4. $M^?$, AP(8), mean 10.3, OR 9.6-11.2, CV 5.8; BL(5), mean 11.7, OR 11.3-12.1, CV 2.6; HC(1), 7.3. dP_4, AP(1), 7.3. M_3, AP(1), 15.2; BL(1), 7.1; HC(1), 6.9.

CONCLUSIONS

Specimens of leptomerycid artiodactyls from the Calf Creek Local Fauna are assigned to the three Cypress Hills Oligocene taxa named by Cope and Lambe.

Hendryomeryx esulcatus teeth are characterized

by small size, low crown height, shallow occlusal pattern, and minor details of crown construction. *H. esulcatus* is not presently recognized in other faunas.

Leptomeryx speciosus, the most common mammalian species at Calf Creek, is intermediate in size and crown height between *H. esulcatus* and *L. mammifer*, and differs from other described leptomerycids in details of crown pattern. *L. speciosus* can be characterized well from the Calf Creek sample, and material from Pipestone Springs, Montana and Flagstaff Rim, Wyoming can be referred with confidence to the taxon.

Leptomeryx mammifer, the largest and highest crowned of the Cypress Hills leptomerycids, is as yet poorly characterized, but it appears that specimens from Pipestone Springs and Flagstaff Rim have been referred correctly to this species.

Presence of *Leptomeryx speciosus* and *L. mammifer* at both Calf Creek and Pipestone Springs gives added similarity to the faunas. But it is not clear how each occurrence fits into the temporal ranges of the taxa.

The Calf Creek assemblage of leptomerycids appears to correlate most closely with the portion of the Flagstaff Rim section (Emry 1973, fig. 18) containing "Species E" (*L. speciosus*) and "Species C" (*L. mammifer*). Size ranges of "Species D" and "Species B" are inappropriate, and "Species A" (*L. yoderi*), although of the same size and crown height as *L. speciosus*, is a taxon consistently different from the Calf Creek taxa in occlusal pattern.

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